

## Antennal Patterns of Sensilla of the Hymenoptera – A Complex Character of Phylogenetic Reconstruction\*

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With 7 figures

### A. Introduction

During the last hundred years, only a small number of publications have dealt with the problems of supraspecific classification and phylogeny of the Hymenoptera. Besides the first attempt towards a higher classification of the Hymenoptera by BÖRNER in 1919, there have been only two entomologists who regarded the different groups analytically in order to come to a detailed knowledge about the genealogical relations between the higher groups.

BROTHERS published in 1975 the results of his studies of different characters from most of the important genera of the Mutillidae, as well as of a limited number of genera of all other groups of Aculeata. He showed a completely closed dendrogram of the Aculeata which is not surprising if we consider the special method which he used; he combined the analysis of characters according to phylogenetic systematics with a special computer program, called a "Wagner tree", based on numerical taxonomy. The combined use of these methods precludes any gaps in his dendrogram (cf. KÖNIGSMANN 1978b). The second approach towards a classification of the higher groups of the Hymenoptera came from KÖNIGSMANN in 1976. His study is based on the results of systematic, morphological or ethological publications of numerous other authors, which is not in contradiction

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\*\*) In memoriam Dr. sc. nat. Eberhard KÖNIGSMANN (1930 - 1980)

to his theoretical method, the phylogenetic systematics sensu HENNIG. In accordance with the aim of phylogenetic systematics he intended to describe the phylogeny of the Hymenoptera only as far as he could find synapomorphic characters. Therefore, he left some problems unsolved, as for example the question of the sister group of the ants, where he could not identify the necessary synapomorphies.

The other important approaches to a natural system of the Hymenoptera which should be mentioned here are the publications of the Hymenoptera catalogues of the world (Genera Insectorum, Hymenopterorum Catalogus), as well as those of different countries. The 1979 published "Catalog of Hymenoptera in America North of Mexico" by KROMBEIN, HURD & SMITH is one example and proves the high standard of systematic research in the United States of America. There is no doubt that one substantial intention of those entomologists who have contributed to these catalogues was the description of a higher classification which should be of course a natural system. The results of these more synthetic approaches have contributed a great deal to our knowledge of the higher classification of the Hymenoptera.

It is not surprising, that there exist a number of different opinions concerning the phylogenetic relationships of most of the distinct groups of the Hymenoptera and a higher classification of this order. So it seems to be necessary to scrutinize the different hypotheses about the relationships of these groups. As we have to assume that one reason for the different hypotheses concerning the phylogenetic relationships of a group is to be seen in the overrating of characters of low complexity which sometimes may be the result of convergent and more often of parallel developments during evolution (cf. HENNIG 1982: 116 ff), we have to search for complex characters (cf. HENNIG 1950: 175) and we must use different methods when studying them.

Some new methods have been introduced into systematic research during recent years from biochemistry, ethology or ultrastructure research. Using for example modern methods like scanning and transmission electron microscopy (SEM and TEM), we may recognize a number of new characters, as has been demonstrated recently by MEINECKE (1975), PAULUS & SCHMIDT (1977), RIEGER & TYLER (1979), STORCH (1979) TYLER (1976) and WACHMANN (1977).

During my studies of the morphology and ultrastructure of the antennal sense organs of *Formica rufa* L. (WALTHER 1981b), the question arose relatively early whether these antennal sense organs may be used as characters for phylogenetic studies concerning the problem of the still unknown common ancestor of the ants. First discussions with Dr. KÖNIGSMANN in 1977 encouraged me to study the antennal sense organs of some selected aculeate Hymenoptera (WALTHER 1979a). Since the results have been very interesting I have continued these investigations during the last six years. On the basis of the results of these studies, which will become published shortly, I am able to give the following description and rating of this complex character.

## B. Inventory of the character "pattern of sensilla"

The results of previous studies of the antennal sense organs (WALTHER 1979a, 1981a) seem to confirm that the antennal patterns of sensilla are characters of high complexity which include a number of variable subcharacters. Some of these subcharacters show more stability towards modifications than other. There exist a great number of possible modifications of many of the subcharacters which makes the whole character so impressive. In a first step we may separate these subcharacters into one group, consisting of the distribution of the sensilla of the different types and their patternlike arrangement on the surface of the antennae, as well as the density of the sensilla of all types or of only one special type, and in another group which includes the morphological and ultrastructural subcharacters of the different types of sensilla.

### 1. Densities of sensilla and patternlike arrangements

The density of sensilla of all types is one subcharacter for which we can easily obtain results by SEM or even by light microscopical studies of bleached antennae. If we compare for example the antennal patterns of sensilla of the cedar wood wasp *Syntexis libocedrii* RONWER (Syntexidae) with that of the fossorial wasp *Myzinum maculatum* (F.) (Myzinidae), it is evident that there are strong differences concerning the density. On the flagellae of the male of *Myzinum maculatum*, we can find a density of all sensilla of 12 sensilla / 1000  $\mu\text{m}^2$  which is ten times higher than those on the flagellae of *Syntexis libocedrii* with about 0,6 sensilla / 1000  $\mu\text{m}^2$  (Fig. 1). There exist not only differences in the density of all sensilla between two distantly related genera which are classified in different families or even superfamilies like *Myzinum* and *Syntexis*. Even within a single family differences exist concerning the density as it has been described for the ants (WALTHER 1981b), where we can find densities of all sensilla between 6 and 15 sensilla / 1000  $\mu\text{m}^2$ .

The density of the sensilla of a special type should be studied at least by SEM, better by combined use of both SEM and TEM. The study of antennal sensilla from different types with the light microscope after bleaching the antennae bears too many possibilities for misidentifications of sensilla with similar hairs which belong to different types.

A high or low density of sensilla of a special type is usually related to a special distribution and arrangement of the sensilla of the different types on the flagellae. There exists no species in the Hymenoptera which shows on its antennae a homogenous distribution of the sensilla of all types. At present we do not know very much about the functional implications of the different distributions and arrangements on the antennae. It is obvious that we find very often a remarkable increase of sensilla of some types from proximal to distal on the flagellae. The reason for this is clear, as the sensilla on the distal antennal segments are more exposed to the surrounding air.

In some monophyletic groups such as the Thynnidae, Myzinidae or Scoliididae we may detect that during the evolution of these groups the distribution and arrangement, as well as the density of sensil-

la of different types has changed - the decrease of the sensilla of one type is usually correlated to an increase of the sensilla of another type.

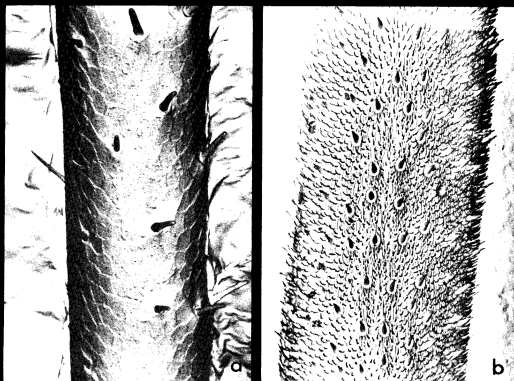


Fig. 1: Different densities of sensilla occur on the antennae of (a) *Syntexis libocedrii* ROHWER, ♀, (Syntexidae) and (b) *Myzinum maculatum* (FABRICIUS), ♂, (Myzinidae). - (a 600x; b 200x).

The developments in distribution and density are mostly connected to an increase or decrease of the dimensions of the cuticular apparatuses, i. e. the hairs, pegs or plates become smaller or greater. We must believe that these alterations of the morphology are accompanied by those of the ultrastructure, as for example in the pore density and structure. These developments began usually in the female sex and continued later in the male sex. The species of *Meria* (Myzinidae) and of *Proscolia* (Scoliidae) possess in the males relatively primitive patterns of sensilla whereas in the females we can see clearly reductions of the height of the hairs and pegs and a decreasing number and density of sensilla. In higher evolved genera such as *Bradynobaenus*, we can recognize in both sexes very smooth antennae and even in the male a reduction of the dimensions of the hairs and pegs, whereas the pore plates of the sensilla placodea are extremely long.

The distribution and arrangement of the sensilla on the antennae may be linked to its morphology, as for example in the males of the conifer sawflies (Diprionidae) (Fig. 2d) where each segment of

the flagellae is branched on two sides. The olfactory Sensilla trichoidea are located only on the branches, whereas the tactile hairs occur mostly on the antennal axis.

In both sexes of the web-spinning sawflies *Megalodontes cephalotes* F. (Megalodontidae) (Fig. 2c) we can recognize a similar distribution of the sensilla even when the branches of the flagellae are comparatively shorter.

A special distribution of the sensilla of the different types is to be seen on the antennae of the horntails (Siricidae), wood wasps (Xiphydriidae) and cedar wood wasps (Syntexidae). In contrast to the leaf-rolling sawflies of the genera *Pamphilius* and *Cephalcia* (Pamphilidae) where the tactile hairs are spread over the whole surface of the antennae, we can see on the antennae of the Siricidae and of some of the Xiphydriidae more or less homogenous fields of olfactory Sensilla basiconica. The tactile hairs and the pegs in pits (Sensilla coeloconica) are located at the periphery of these fields (Fig. 2a). On the antennae of the cedar wood wasps (Syntexidae) we may recognize a clear separation of the sensilla with pegs and hairs from those with plates.

The separation of the sensilla of the different types on the antennae of the parasitic wood wasps (Orussidae) is less clear, even when the chemosensitive sensilla are concentrated on one half of the antennal segments. Tactile hairs are to be seen on nearly all parts of the antennae.

The distribution of sensilla on the flagellae of the xyelid sawflies (Xyelidae) is also clearly correlated with the morphology of the flagellae. The third antennal segment of the female of *Xyela* sp. is extremely long and thicker than the other distal segments (Fig. 2b). According to one opinion, it has developed during evolution by a fusion of seven smaller antennal segments (cf. KÖNIGSMANN 1977). A great number of sense organs with long and slender plates occur only on this third antennal segment. They seem to be an kind of Sensilla placodea and we may presume that they have an olfactory function. In contrast, we find on the distal antennal segments numerous sensory hairs which may belong to mechanosensitive sensilla.

The following examples of special patterns and distributions of sensilla are not recognizable depending on a special morphology of the flagellae. They show usually the normal cylindrical structure of each segment.

On the antennae of female cuckoo wasps of the genus *Cleptes* (Clepidae), the olfactory Sensilla trichoidea are concentrated in a field proximal of the Sensilla basiconica.

On the flagellae of female velvet ants (Mutillidae) and of most of the female Myzinidae and Thynnidae in contrast, the Sensilla trichoidea are situated between the Sensilla basiconica.

The pattern of sensilla of the male *Sierolomorpha canadensis* (PROVANCHER) (Sierolomorphidae) is characterized by a great number of Sensilla coeloconica (pegs in pits) which are spread over at least one half of the surface of the antennal segments. The high number of these sensilla is especially remarkable, as in no other genus of the Aculeata which has been studied so far, such a high number

of these sensilla has been found.

The concentration of some Sensilla coeloconica (pegs in pits) in a small area is not unusual. The males of *Formica rufa* L. (Formicinae) possess on their distal antennal segments lateral a small field of about 15-20 Sensilla coeloconica (WALTHER 1981b). Males of the genera *Myzinum*, *Mesa*, *Meria* and *Dermasothus* (Myzinidae) show also such a concentration of Sensilla coeloconica in the ventrolateral region of their antennal segments (WALTHER 1979a, in prep.)

The females of *Brachycistis carinata* FOX (Brachycistididae) possess on their antennal flagellae in the dorsal part a troughshaped area in which the olfactory Sensilla basiconica and Sensilla trichoidea are situated, - well preserved but insufficiently exposed to the surrounding air.

A remarkable pattern of sensilla is to be seen on the flagellae of the males of *Diamma* (Thynnidae), *Myzinum*, *Mesa*, *Meria* (Myzinidae) and of different genera of the Pompilidae; in the dorsal half of the flagellae, a number of thick cone-shaped tactile hairs with a grooved surface are situated between the rows of the long and slender Sensilla placodea and numerous olfactory Sensilla trichoidea (Fig. 1b).

Numerous olfactory Sensilla trichoidea, which are arranged in variously formed patches occur on the antennal flagellae of the males of the Thynninae (Thynnidae), of *Fedschenkia* (Fedschenkiidae) and *Dermasothus* (Myzinidae).

The placoids on the antennae of male wasps of the genera *Sphex* (Sphecidae), which are special taxonomic characters (BOHART & MENKE 1976), consist also of numerous olfactory Sensilla trichoidea, concentrated in long troughs on the dorsal half of some of the different antennal segments.

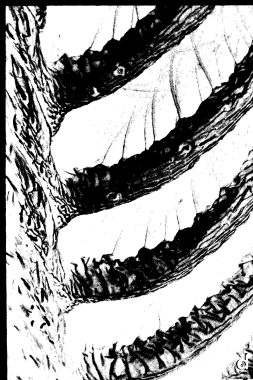
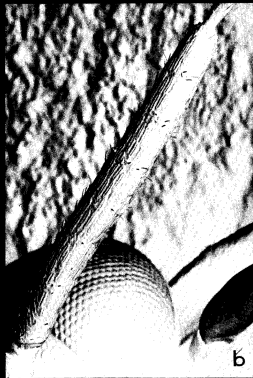
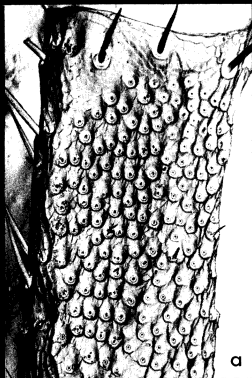
## 2. Morphology and ultrastructure of sensilla

The morphology of the cuticular apparatuses of the different types of sensilla may be also helpful as subcharacters for the study of phylogeny.

The olfactory Sensilla basiconica (Fig. 3) possess cuticular appa-

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Fig. 2: (a) The olfactory sensilla on the antennae of *Sirex nitobei* MATSUMURA, ♀, (Siricidae) are concentrated in a field and surrounded by some tactile hairs. - (b), On the third antennal segment of *Xyela* sp., ♀, (Xyelidae), numerous plates are to be seen which may belong to Sensilla placodea. - (c) The olfactory sensilla are only concentrated on the branches of the antennal segments of *Megalodontes cephalotes* FABRICIUS, ♀, (Megalodontidae) and (d) *Diprion pini* (L.), ♂, (Diprionidae). - (a 220x; b 140x; c 260x; d 240x).



ratusses, which consist always of a peg on a socket. The structural variability of these two parts of the cuticular apparatus is remarkable. It seems that Sensilla basiconica with short and cylindrical pegs which are standing in the center of a socket with a great diameter are more primitive than those with slender and long pegs placed on small sockets. The pores of these sensilla are arranged on the top of these cylindrical pegs. More highly developed Sensilla basiconica may show, for example, a peg asymmetrically placed on an elliptic socket. Other sensilla of this type, which are more highly evolved, have long and thin pegs. Their pores are distributed over the distal and also in part on the lateral regions of the pegs.

The olfactory Sensilla trichoidea (Fig. 4) of different genera are often very similar. Structural differences occur mostly at the socket. Sometimes we find shorter hairs, which have in some cases rounded tips.

The pore plates of the olfactory Sensilla placodea (Fig. 5) show great structural variability. Long and slender forms, as well as round and elliptic ones occur, sometimes even on the antennae of one sex

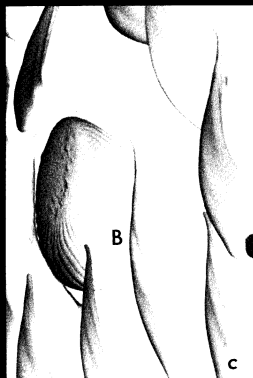
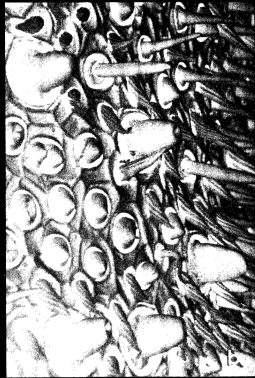
The Sensilla trichoidea curvata of the ants, which are homologous to the Sensilla placodea of other Aculeata, possess in most species a hair-like pore plate (WALTHER 1981b). The name Sensillum trichodeum curvatum of this type of sensillum calls to mind superficial similarities with the other olfactory Sensilla trichoidea, but without any doubt, they are the result of convergent developments. The arrangement of the pores in double rows, as well as the well developed cuticular ledges demonstrate clearly that they are homologous to the other Sensilla placodea.

Another direction is to be seen on the flagellae of the archaic ponerine ant *Plathythyrea lamellosa* ROGER, where Sensilla trichoidea curvata with very short pore plates, which are relatively similar to those of the long and slender Sensilla placodea of some primitive solitary wasps from the Scolioidea (WALTHER in prep.) can be observed.

The elevation of the pore plates of the Sensilla placodea over the surface of the antennae has developed independently several times during evolution in different genera of different families of the Aculeata, as for example on the antennae of the males of *Myrmosa* and *Kudakrumia* (Myrmosidae), the males of *Loboscelida* (Loboscelidae) and of *Plumaroides* (Plumariidae). The males of *Eotillia* (Eotillinae) and the males and females of *Typhoctes* (Typhoctinae) and *Chyphotes* (Chyphotinae) show also Sensilla placodea with elevated pore plates on their flagellae. It seems to be very probable that the advantage of the Sensilla placodea with elevated pore plates is to be seen in the fact that they have a higher absorption coefficient for odorous molecules.

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Fig. 3: The different Sensilla basiconica of (a) *Paravespula vulgaris* (L.), ♀, (Vespidae), (b) *Bembix rostrata* L., ♂, (Sphecidae), (c) *Anoplius viaticus* L., ♀, (Pompilidae), and (d) *Mesa petiolota* (SMITH), ♀, (Myzinidae) belong to the olfactory sensilla. - (a 1340x; b 1320x; c 6000x; d 2400x).



The sense hairs of the gustatory and mechanosensitive Sensilla chaetica usually appear to be very similar. In those species whose pattern of sensilla is reduced and shows shorter cuticular apparatuses, the Sensilla chaetica also have shorter sense hairs. They are normally innervated by five or six sense cells.

The variability of the cuticular apparatuses of the mechanosensitive tactile hairs is remarkable. We know a great number of different forms from extreme thin, thread-like hairs on one hand to thick, cone-shaped peg-like hairs on the other. The surface of many of the thicker hairs is grooved. Structural differences between the distal cuticular apparatuses of the mechanosensitive Sensilla campaniformia are rare. This type of sensillum possesses an extreme high structural stability compared with most of the other types.

Three different types of sensilla belong to the group of the pegs in pits, the Sensilla ampullacea, the Sensilla coeloconica and the poreless pegs (ALTNER & PRILLINGER 1980). In most of the species studied so far, the sense hairs of these types of sensilla are located in round chambers under the surface of the antennae. In some species, where the chamber is situated directly under the surface of the antennae, a distal opening connects the inside of the chamber with the surrounding air. In other species, however, we find the chamber of Sensilla ampullacea and Sensilla coeloconica at a greater depth inside of the antennae. In these cases, a cuticular channel is to be seen between the chamber and the surface of the antennae.

The special location of these sensilla is responsible for the fact that they cannot be easily studied with the SEM. Very often, we find only the small distal openings of the chamber or the channel. Some exceptions exist, as some Sensilla coeloconica, such as those of the conifer sawflies (Diprionidae) (Fig. 7a) and of the chalcid *Monodontomerus obsoletus* F. (Fig. 7b) are not provided with a chamber. Their sense hairs are found on the surface of the antennae. The Sensilla coeloconica of some other species (Fig. 7e-f) can be studied relatively easily with the SEM because of the large distal openings of their chambers. - The poreless pegs occur only in small numbers on the antennae. Therefore, they are not as easily to identify with the SEM (WALTHER 1981b). They include thermo- and hygro-sensitive sense cells (YOKOHARI & al. 1982).

Ultrastructural investigations with the TEM provide us with a number of additional characters and are often necessary to come to be a better functional interpretation of sensilla previously studied with the SEM. Some interesting subcharacters which can be studied only with the TEM are the stimulus transmitting pore structures, as for example pores with pore tubuli or pore channels. My own recent TEM studies of different Sensilla placodea and other olfactory sensilla have demonstrated this. Different pore structures had been described in detail by ALTNER (1977b). They vary also in their special distribution and arrangements.

The dendrites of the sense cells possess a remarkable structural variability which depends mostly on the different modalities of the sensilla (ALTNER & PRILLINGER 1980). The number of sense cells differs also between sensilla of the same type, if we compare species from different genera or families. The olfactory Sensilla trichoidea of the males of *Tiphia femorata* F. are innervated by 4-5

sense cells (WALTHER in prep.), those of the males of *Formica rufa* L. by 8-13 sense cells (WALTHER 1981b).

The number of sheat cells of the different types of sensilla varies between one and six in the Hymenoptera. Even in one type of sensillum as for example in the tactile hairs, we find different numbers of sheat cells after the ontogenesis of the sensilla (WALTHER 1981b). The structure of homologous sheat cells in different types of sensilla also shows some variation.

### 3. Sexual dimorphism in patterns of sensilla

The occurrence of sex specific differences between the patterns of sensilla of males and females of a species is not so outstanding if we consider that in some groups of the Aculeata sexual dimorphism has developed to such an extent, that we can often find males and females of a species together only on one occasion: when they have been caught in copula. Especially in the Mutillidae and Tiphiidae sensu PATE, as well as in the Bethyidae, we find strong sexual dimorphisms. It seems to be evident that this fact can be of great advantage, as we are so provided with two independent arrays of characters (WASBAUER 1968).

The sex specific differences of the patterns of sensilla of a species include different numbers of types of sensilla, different densities of sensilla, variations concerning the patterns and distributions of sensilla, as well as structural and ultrastructural differences of the types of sensilla. Another important moment, which has to be considered when using the patterns of sensilla for the reconstruction of phylogeny, is the fact that the males in the Hymenoptera often show the more primitive expression of a character. This had been mentioned before by KÖNIGSMANN (1978c) for the ants, but it seems to be the rule for all Hymenoptera. This means that, for phylogenetic studies, the pattern of sensilla of the males often show a lower character condition in their transformation series, than those of the females. This may sometimes be an advantage, as it probably permits us to find conformities with other species or genera based on the subcharacters of the pattern of sensilla of only one sex.

## C. Discussion

Intensive studies of the antennal patterns of sensilla of various Hymenoptera during the last years have repeatedly confirmed the assumption that this complex character may be very valuable for the reconstruction of phylogeny. The remarkable attribute of the character pattern of sensilla, which is composed of different subcharacters, some of which contain a special pattern and distribution component and some a morphological and ultrastructural one appears to be of particular importance. The components making up this character support the conjecture that this is a polygenetic character.

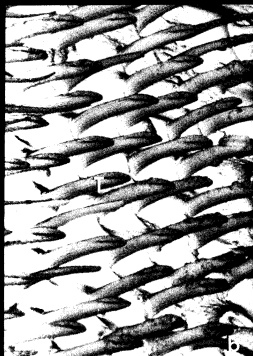
The most successful method for studying the antennal patterns of sensilla seems to be the combined use of scanning and transmission

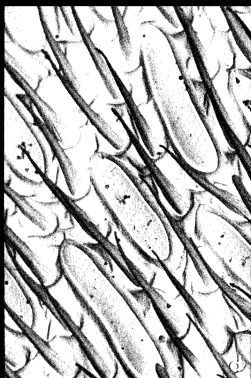
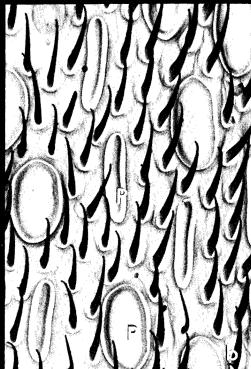
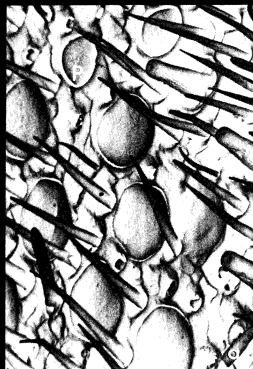
Fig. 4: The olfactory Sensilla trichoidea of (a) *Rhopalosoma nearcticum* (BRUES), ♀, (Rhopalosomatidae), (b) *Cleptes fudzi* TSUNEKI, ♀, (Chrysidae), (c) *Plumarioides andalgalensis* BROTHERS, ♂, (Plumariidae), and (d) *Smicromyrme bareyi* RADOSZKOWSKI, ♂, (Mutillidae) have very similar sense hairs. - (a 2000x; b, c, d 2200x).

Fig. 5: The pore plates of the olfactory Sensilla placodea of (a) *Tiphia femorata* FABRICIUS, ♀, (Tiphidae), and (b) *Mesa petiolata* (SMITH), ♀, (Myzidae) belong to two different types. This seems to be a special subcharacter of the patterns of sensilla of different genera of the Scolioidea. - (c) On the flagellae of *Monodontomerus obsoletus* FABRICIUS, ♀, (Chalcidoidea), and (d) *Paravespula vulgaris* (L.), ♀, (Vespidae), we can see different forms of long and slender pore plates of two types of Sensilla placodea. - (a 1320x; b 1100x; c 1200x; d 1340x).

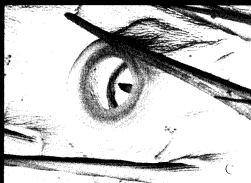
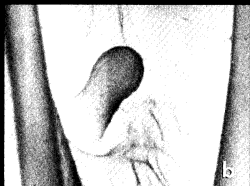
Fig. 6: The different structures of the tactile hairs of (a) *Anoplius viaticus* L., ♂, (Pompilidae), (b) *Anthobosca chilensis* (GUÉRIN), ♂, (Anthoboscidae), (c) *Pseudogonolobus hahni* SPINOLA, ♀, (Trigonidae), and (d) *Plumarius* sp., ♂, (Plumariidae) are remarkable subcharacters. - (a 1760x; b 2000x; c 1200x; d 200x).

Fig. 7: Sensilla coeloconica occur on the surface of the antennae, as well as in cuticular chambers under the surface. The differences concerning the cuticular apparatuses of the Sensilla coeloconica (a) of *Neodiprion sertifer* (GEOFFROY), ♀, (Diprionidae), (b) *Monodontomerus obsoletus* FABRICIUS, ♀, (Chalcidoidea), (c) *Rhopalosoma nearcticum* (BRUES), ♀, (Rhopalosomatidae), (d) *Olixon banksii* (BRUES), ♂, (Rhopalosomatidae ?, Pompilidae ?), (e) *Ophion luteus* L., ♀, (Ichneumonidae), and (f) *Brachycistis carinata* FOX, ♂, (Brachycistidae) are remarkable. - (a, b, e 6000x; c 2000x; d 5000x, f 2200x).









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electron microscopy (SEM and TEM). Sometimes, especially in case of pegs in pits, it may be useful to study some bleached antennae with the light microscope. The application of SEM and TEM methods provides us with much detailed information, much superior to that which we could obtain by using only light- and stereo microscopy. Another great advantage of the SEM method is the possibility of using dried specimens from the collection. This permits us to study also rare species which are generally not available as living material for TEM studies, but often very important if they belong to small genera or families. It must be mentioned, however, that the SEM method alone does not always allow us to come to a functional interpretation of the results. Questions concerning innervation or the stimulus transmitting structures of the sense organs must first be answered, if we want to understand the function or modality of a sensillum. This makes intensive TEM studies of at least some of the species under concern necessary. The supply of living material of special species for these TEM investigations is often a great problem and we generally must study specimens of those species which are available.

In recent years, some objections have been put forward against the use of the patterns of sensilla as characters for phylogenetic reconstructions. Some researchers have maintained that sense organs are always under such a strong adaptive pressure that they react too easily with structural modifications. This would support rejecting their use as characters for phylogenetic studies, because of the possibility that they may form parallelisms or convergences too quickly. With regard to this assumption, it appears interesting that MOULTON & BEIDLER (1967) and TOBACH (1971) have been able to demonstrate that special adaptations in sense organs are most often to be found on the molecular level of the receptor cell or in the processing of information in the central nervous system. The following comment of GLEESON (1978) supports this view with respect to a special group of sense organs when he writes: "Although functional adaptations of the chemical senses are quite diverse, these adaptations are not reflected in a comparable number of morphological modifications of the receptors themselves or their accessory structures".

On the base of the results of my own previous studies, I can neither reject the use of sense organs as characters in phylogenetic studies because of the danger of convergences and parallelisms as a result of the high adaptive pressure, nor can I accept the assumption of GLEESON, that there does not exist an adequate number of modifications resulting from diverse functional adaptations.

The question of whether we should make a choice between different characters and exclude those which seem to be under a special adaptive pressure as a result of their important role in the life of the organisms has been discussed intensively by HENNIG (1950, 1979, 1982). In contrast to his earlier statements (HENNIG 1950: 178 ff), in which he supports the opinion of MICHAELSEN (1935), that completely unimportant characters ... "are disproportionately important in systematics", HENNIG (1979, 1982: 119 ff) later explains that systematists have to consider all characters and he continues "that it is not the characters themselves, that are important in systematics, but their relations to other characters in a transformation series - whether they represent plesiomorphous or apomorphous conditions". There is no doubt that HENNIG changed his standpoint concerning this problem. The "criterion of correspond-

ing special characters" (HENNIG 1950: 178) has been dropped in the new editions (HENNIG 1966, 1979, 1982). It seems that this new standpoint of HENNIG has not found the necessary attention of all researchers. According to these explanations of HENNIG, we have to take into consideration that high stable characters (MICHAELSEN 1935) which do not show any development cannot be a component of a transformation series and thus are useless for the reconstruction of phylogenetic relations.

The problem of convergences and parallelisms has been also discussed comprehensively by HENNIG (1979: 117 ff, 1982: 116 ff); short but detailed explanations have been given by KÖNIGSMANN (1975). Therefore, we may limit the discussion to the special situation of the character pattern of sensilla.

On the basis of our previous results we can show that in different monophyletic groups of the Aculeata some unidirectional developments for which we could also use the terms "orthogenetic series" or "trends" (HENNIG 1979, 1982) doubtlessly exist. It is clearly visible that these transformation series take a parallel course, as for example the trends to develop very smooth antennae, which show sensilla with reduced hairs, pegs etc. in the Myzinidae, Sco-liidae, Brachycystiidae, and Bradynobaenidae.

However, the complexity of the character pattern of sensilla, consisting of the different subcharacters mentioned above, is also of great advantage in distinguishing these parallel transformation series. Enough different subcharacters occur between them, when we compare similar transformation conditions.

In this connection, we have to also keep in mind the recommendation of HENNIG (1979, 1982: 121), who has pointed out that the occurrence of parallelisms and convergences makes the investigation of different characters necessary; one should include as many different characters as possible in a phylogenetic study. The great number of different subcharacters, which make up the complex character pattern of sensilla, should not prevent us from studying additionally other characters.

The aim of these investigations of the patterns of sensilla is, firstly to support or deny existing hypotheses, such as those of BROTHERS (1975) and KÖNIGSMANN (1976, 1977, 1978a, b), and in a second step, if necessary, to establish new hypotheses.

Concerning the first intention of these investigations, some workers have objected that the patterns of sensilla represent only one character in contrast to investigations such as those of BROTHERS and KÖNIGSMANN, whose hypotheses are based mostly on different characters. In our opinion, these researchers do not rate correctly the value of the high complexity of this character and we must again call to mind the sexual dimorphisms of the patterns of sensilla, which very often provide us with two independent transformation series, so that we must always study, if possible, both sexes of a species. When we consider the second intention of these studies, the formulation of new hypotheses, it is obvious that we must also study other transformation series when we later examine these new hypotheses based on the results of the investigations of the patterns of sensilla. To check whether the hypotheses based on the study of independent transformation series can be brought into congruence, we have to apply the principle of reciprocal clarifi-

cation (HENNIG 1979, 1982).

An additional result of these investigations is that we are provided with much information about the evolution of form (HENNIG 1979, 1982) of the character pattern of sensilla, which can help us, using also the principle of reciprocal clarification, to "disclose the phylogenetic kinship of related groups".

Another aim of these investigations is to learn more about the orientation of some Hymenoptera with the aid of their antennal sensilla. Most of the previous functional morphological and ultrastructural, as well as sensory physiological studies, have concentrated on a small number of species. As a result of these studies, a number of questions have arisen concerning the efficiency of these different patterns of sensilla. Unfortunately, our knowledge of the behaviour and biology of most of the species of the Aculeata is at present quite limited.

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